Larval dispersal simulations and connectivity predictions for Mediterranean gorgonian species: sensitivity to flow representation and biological traits

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July 4, 2022

Abstract

Larval dispersal enables demographic and genetic connectivity among marine populations. For many sessile species, it is the only natural mechanism for resilience after major population disturbances, as those that have been affecting Mediterranean gorgonian species inside and outside MPAs. Larval dispersal simulation is a powerful tool to anticipate connectivity among populations which might be altered by modelling choices. We assessed how flow representation (resolution and vertical turbulence) and larval traits (pelagic larval duration, release timing and duration, larval vertical behaviour) influenced populations connectivity among five coastal rocky locations in the Northwestern Mediterranean, four of them being designated as MPAs. We used a finer (0.3 km) and coarser (1.5 km) flow resolution in two years to asses, using a hierarchical simulation approach, the sensitivity of connectivity patterns to the above parameters. Larval traits corresponded to two gorgonian species, the neutrally buoyant *Eunicella singularis* and the passive sinker *Paramuricea clavata*. Ocean model resolution was the most influential factor on resulting connectivity patterns. When using the finer flow model resolution, connectivity patterns were equally influenced by all larval traits while vertical turbulence could be neglected. Hence, advising the design of coastal MPAs with regional connectivity estimates requires adequate flow simulation resolution.

Keywords: Larval dispersal modelling; connectivity; larval behaviour; larval traits; NW Mediterranean; *Paramuricea clavata*; *Eunicella singularis*

1 Introduction

Anticipating the impact of the on-going global change on the already altered ocean biodiversity is a major challenge for designing conservation measures for the next decade (ONU

SGD 14, IPBES 2030 work program). Among conservation measures, the Aichi Convention on Biological Diversity (CBD, 2010) defined the objective of reaching 10% of ocean surface designated as Marine Protected Areas (MPAs) by 2020. Many studies have shown the efficacy of MPAs on the conservation of fishes and benefits to outside areas through the spillover of juvenile and adult fishes (see Grüss et al., 2011, for a review). MPAs actually conserve habitats in which motile species find food and/or refuge by being geographically confined. An essential component for MPAs attractiveness is the presence of large erected sessile species like corals and gorgonians as they increase habitat complexity and are associated to abundant and diverse vagile species (Ponti et al., 2016). Along the Mediterranean coastline, many gorgonian populations have been reported, outside and inside MPAs. These ecosystem-engineer sessile species are therefore considered as umbrella species and used as indicator of conservation measures efficacy by MPA managers. Yet, the conservation in MPAs of sessile species whose reproduction implies a dispersive phase mediated by ocean flow poses the question of anticipating population renewal, hence connectivity, within a geographically fragmented network (Halpern and Warner, 2003). Extending or modifying the existing network of MPAs requires performing scenarios based on sounded scientific knowledge (MedPAN, 2017). Designating efficient MPAs requires incorporating knowledge and understanding of mechanisms regulating species spatial distribution, including dispersal (Urban et al., 2016).

To this end, larval dispersal numerical models allowing to incorporate knowledge and understanding of mechanisms regulating dispersal are essential tools (Lett et al., 2008; Paris et al., 2013). However, in practice, larval dispersal simulations first require flow simulations to provide a reliable and validated flow representation. Flow variability should be accounted for at spatio-temporal scales relevant for both dispersal processes (larval scale) and regional connectivity estimates (population scale, including demographic variability, North et al., 2009). Connectivity studies have used a variety of ocean circulation models, from coarse-resolution global models (10 km, Wood et al. 2014) to high-resolution regional models (100 m to 1 km, Guizien et al. 2012; Briton et al. 2018). Ocean flow models have been validated against diagnostic variables such as sea surface temperature

and salinity, heat content and sea level. However, such validation can be insufficient to ensure that simulated velocities used in the larval dispersal simulations are representative of the advection and diffusion experienced by larvae in the flow (Pineda et al., 2007). When the flow field (speed and direction) simulations are accurate, the specificity of larval dispersal simulations ultimately depends on the knowledge of biological traits such as location and timing of larval release in parental populations and larval traits important for dispersal (Scheltema, 1986). For benthic species, combining underwater imaging techniques with species distribution modelling enables to significantly expand knowledge about parental populations mapping and is now frequently used to parameterize larval dispersal simulations, including those in deeper environments (Metaxas et al., 2019). In contrast, release schedule within the reproductive season is often not known, due to the difficulty of observing such inconspicuous events (except for massive spawners such as corals, Coelho and Lasker, 2014). A recent systematic study of the sources of variance in recruitment patterns along the Chilean coast suggested that nearly half of the variance remained unexplained by PLD, behaviour, release location or season, pointing out to the significance of hydrodynamic stochasticity in coastal wind-driven flows in connectivity patterns (Ospina-Alvarez et al., 2018). Varying the timing of pulse release events within the reproductive season have shown that short term variability in wind-driven flows drives large differences in larval dispersal patterns (Marta-Almeida et al., 2006; Guizien et al., 2012). In presence of short term flow temporal variability, repeating short release events periodically or extending the release duration is essential to increase the persistence of population connections (Guizien et al., 2012; Kough and Paris, 2015; Hock et al., 2019). Once release location and timing are defined, Pelagic Larval Duration (PLD, hereinafter), considered as a primary driver of connectivity, has been extensively tested in larval dispersal simulations (, reviewed in Swearer et al. 2019). When the PLD was varied, larval dispersal either relied on the neutrally buoyant larvae approximation in three-dimensional simulations (Guizien et al., 2012; Simons et al., 2013) or was restricted to two-dimensional simulations at a fixed depth, often at the surface (Gamoyo et al., 2019). However, larval position in the water column is critical for the dispersal of many benthic species taxa

(Corell et al., 2012) and traits regulating the vertical position of benthic species alter their dispersal (Queiroga et al., 2007). Including larval motility behaviour in dispersal modelling requires knowledge on the behaviour of larvae of the species of interest, which implies bridging a gap between modelling and experimentation (Leis, 2021). In summary, the impact of flow field representation choices on connectivity estimates needs to be assessed systematically and compared to the effect of varying biological traits (Huret et al. 2007).

In the present study, we performed a case study for larval dispersal simulations sensitivity analysis for two Mediterranean gorgonian species, *Paramuricea clavata* (Risso 1826) and *Eunicella singularis* (Esper 1794). We selected five locations in the Ligurian sea where gorgonians have been reported. Four of these locations are designated as MPAs. We addressed first the sensitivity of connectivity predictions among these five locations to flow representation, including horizontal grid resolution and temporal resolution, together with varying basic dispersal parameters such as PLD, release timing and duration. We addressed then the sensitivity to traits regulating larval vertical position, with and without turbulent vertical diffusion. Eventually the sensitivities to the different parameters were ranked by importance and commented with respect to connectivity estimates within the current MPA network of the Ligurian Sea.

2 Methods

2.1 Study background

The Ligurian Sea extends between Italy and the north of Corsica in the Northwestern Mediterranean Sea. It is characterized by a mean cyclonic circulation (Millot, 1999) known as the Ligurian Current (LC) that flows west along the Italian coast toward France (Fig.1). The Ligurian Current is a well studied component of the large scale Mediterranean circulation, however only a very limited number of flow speed observations are available in the summer season along the coastline. We used for validation a time series from an Acoustic Current Doppler Profiler (ADCP) deployed in 2004 in the vicinity

of the MT Haven shipwreck (44.37^{o}N, 8.70^{o}E, Fig.1, open triangle).

Along the Ligurian coast, many MPAs have been established (Regional Natural Reserve of Bergeggi, Regional Natural Park of Portofino, Cinque Terre National Park, Regional Natural Park of Porto Venere, Fig.1). These MPAs foster the conservation of the rich biodiversity associated to the patchily distributed coralligeneous and rocky bottom habitats. In these MPAs, conspicuous gorgonian species such as *Eunicella singularis* and *Paramuricea clavata* have been used as flagship species for the conservation of the Mediterranean coralligeneous assemblage (Carpine and Grasshoff, 1975), due to their role of ecosystem engineer (sensu, Jones et al. 1994), and their patrimonial value linked to their beauty.

The white gorgonian *Eunicella singularis* is an erected sessile species of about 50 cm height which dwells on rocky bottoms in shallow waters, as well as on coralligenous formations in deeper sublittoral waters (Gori et al., 2011). Each year, *E. singularis* releases lecithotrophic planulae during periods of about 10 days between the end of June and early July (Ribes et al., 2007). *E. singularis* larvae swim during 45 to 91% of the time, compensating for their negative buoyancy. In a laboratory experiment, these larvae maintained themselves at 20°C in the middle of the sea water container, just like neutrally buoyant larvae (Guizien et al., 2020).

The red gorgonian *Paramuricea clavata* is one of the tallest sessile Mediterranean species with erected colonies as high as 1.3 m and is found on hard substrate from 10 to 200 m water depth (Gori et al., 2017). During reproduction, *P. clavata* releases eggs that get fecundated and maturate within a few days at the colony surface. Once the maternal mucus is dissolved, lecithotrophic planula larvae are released in the ocean flow. *P. clavata* larvae are non-motile and sink in sea water at 20°C (Guizien et al., 2020). Off the Catalan coast, larval release happens during short events of a few days separated by 15 days (Coma et al., 1995; Gori et al., 2007) in late June/early July. No information on the exact timing and occurrence of *P. clavata* larval release in the Ligurian Sea are available in the scientific literature but several observations by recreational divers report a similar phenomenon in the month of July. For the two species, the competency period

117 extends from a few days to more than 30 days (Guizien et al., 2020; Zelli et al., 2020).

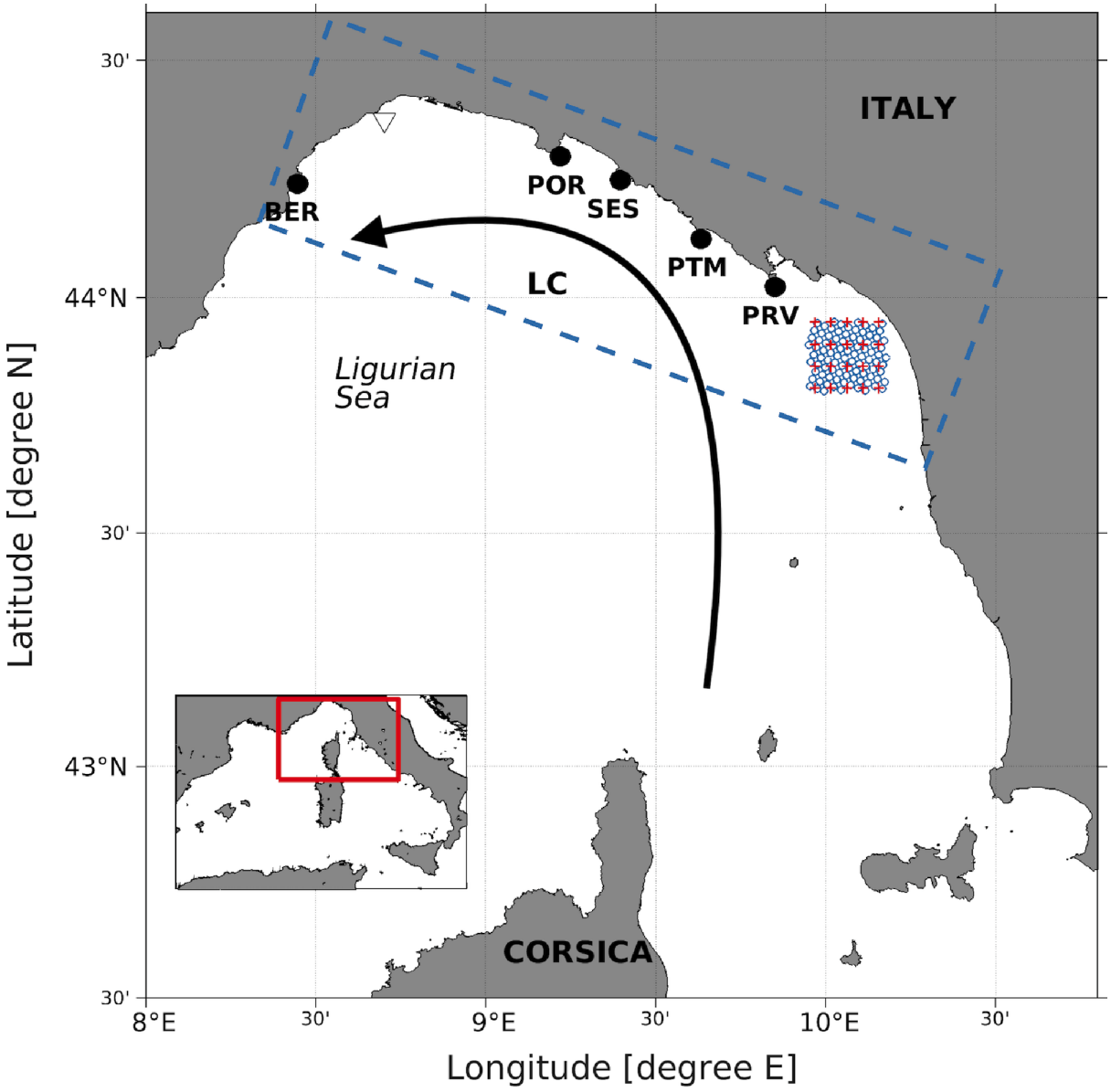

Figure 1: The Ligurian Sea. The arrow depicts the main circulation branch and black circles indicate the release locations used in larval dispersal simulations (see Tab. S1 in the Supp. Inf. for the precise locations). The open triangle indicates the location of the Acoustic Doppler Current Profiler used for flow data validation. Blue dashed rectangle shows the LIMEgcm (fine resolution) domain while the red rectangle in the inset shows the LIME-ROMS (coarse resolution) domain. Blue circles display every 6 grid points of the the LIMEgcm mesh and red crosses display every 3 grid points of the LIME-ROMS mesh.

2.2 3D flow simulations at coarse and fine resolutions

The circulation of the Ligurian Sea was simulated at two grid resolutions in 2004 and 2006, with the aim of describing the inter-annual variability in the stratified summer circulation while limiting the number of simulations. In fact, the largest deviation in the Mediterranean summer sea surface temperature over the $2003-2019$ period was observed between 2004 and 2006 (García-Monteiro et al., 2022) and an abrupt shift in the Western Mediterranean circulation was observed starting from 2005 (Schroeder et al., 2016).

The coarser resolution 3D flow simulations hereinafter called Ligurian Integrated Modelling Effort-ROMS (LIME-ROMS, Sciascia et al. 2019) was based on the Rutgers University kernel of the Regional Ocean Modelling System (ROMS, Shchepetkin and McWilliams 2005). The numerical domain was discretized with an horizontal grid of 590 x 314 points. The mesh was unevenly spaced and the most resolved area (Fig.1, red rectangle), which includes the area of the Ligurian-Northern Tyrrhenian shelf, had a horizontal resolution of 1/64° x 1/64° ($\sim$ 1.5 km, Fig.1, red crosses). The vertical dimension was discretized with 50 sigma layers. Realistic surface forcings came from the 3-hourly, 0.25° horizontal resolution ERA-Interim reanalysis fields (Dee et al., 2011), while the daily open boundary values were derived from the Mediterranean Forecasting System (MFS) SYS4a3 product. Model outputs were saved every six hours. The reader is referred to Sciascia et al. (2019) for a detailed description and evaluation of the hydrodynamical model performance.

The fine resolution 3D flow simulations hereinafter called Ligurian Integrated Modelling Effort gcm (LIMEgcm, Fig.1 blue dashed rectangle) was based on the Massachusetts Institute of Technology general circulation model (MITgcm, Marshall et al. 1997). The MITgcm solves the Boussinesq form of the Navier–Stokes equations either on a generalized curvilinear grid or an orthogonal grid. The finite-volume discretization is rendered on a horizontal Arakawa C-grid with vertical z levels. In this configuration the equation of state is due to Jackett and McDougall (1995) and the advection of tracers is computed via a third-order direct space–time flux limited scheme with zero explicit diffusivity. The K-profile parameterization (KPP, Large et al. 1994) is used with a background vertical

viscosity of 10^{-5} m^2s^{-1}. The numerical domain was discretized with an orthogonal horizontal grid of 560 x 160 points. The horizontal mesh had a resolution of 300 m (Fig.1, blue circles) while the vertical was discretized with 100 levels. The vertical resolution increased linearly from 1 m to 20 m in the first 20 levels, was kept constant at 20 m for the following 50 levels, and finally increased to 25 m for the 30 deepest layers. The bathymetry is interpolated from the EMODNET 1/8 arcminute product. Realistic surface forcings came from the hourly, Weather Research and Forecasting (WRF) model setup by the University of Genoa (Cassola et al., 2015), while 6-hourly open boundary conditions were derived from LIME-ROMS model outputs (Sciascia et al., 2019). Model outputs were saved every three hours.

2.3 Larval dispersal simulations

Dispersal simulations of virtual larvae were performed independently using the LIME-ROMS (hereinafter, coarse) and LIMEgcm (hereinafter, fine) simulations.

The offline Lagrangian Transport model (LTRANS, Schlag and North 2012) was selected to compute particle advection in the coarse resolution flow field for its capability to cope with sigma layers. The offline Connectivity Modelling System (CMS, Paris et al. 2013) was selected to compute particle advection in the fine resolution flow field for its capability to cope with z layers. Both Lagrangian models compute 3D trajectories using a 4th-order Runge-Kutta scheme and can describe neutrally buoyant and active (e.g. sinking, swimming) particles, eventually including horizontal and/or vertical turbulent diffusion to represent horizontal and/or vertical motions at scales smaller than the grid resolution of the flow models.

In the present study, particles were released in five locations Bergeggi (BER), Portofino (POR), Sestri Levante (SES), Punta Mesco (PTM), and Porto Venere (PRV), all being MPAs except SES (Fig. 1, Supp. Inf. Tab. S1). Each location was described by ten release points, separated by 100 m. Particles were released $\sim$ 3 km away from the coast line and 4 m above the bottom in the coarse resolution simulations and 2 m above the bottom in the fine resolution simulations in order to avoid any retention bias due to the

bottom numerical boundary layer (Supp. Inf., Tab. S1). In all larval dispersal simulation setups, particles were tracked with a tracking time step of 600 s, ensuring that no particle crossed a grid cell within one timestep at the fastest flow speed.

The hierarchical simulation design used in this study consisted of eight larval dispersal simulation experiments (Tab. 1). In a first group of experiments, the effect of the flow field representation (in space and time) was quantified for neutrally buoyant particles by comparing purely Lagrangian simulations using both the coarse and fine resolution flow representation, the latter varying the flow update frequency between 6h and 3h (Exp. 1, 2 and 3 in Tab. 1). In a second set of experiments, the effect of the different larval vertical behaviour of two gorgonian species and vertical turbulence were quantified applying a fully factorial set up (from Exp. 3 to 8 in Tab. 1). In this case, only the fine resolution flow representation was considered as it was shown to best agree with current speed observations in the area and Exp.3 was considered as reference simulation (see Results section). In all larval dispersal simulation experiments (from Exp. 1 to 8, Tab. 1), particles were released every hour from June 15 at midnight until July 15 at 11 pm for both 2004 and 2006 and tracked for 28 days, according to their competency ability (Zelli et al., 2020).

The neutrally buoyant particles would actually represent the motile *E. singularis* larvae, which swimming behaviour compensates their negative buoyancy (Padrón et al., 2018a). The non-motile *P. clavata* larvae (Coma et al., 1995; Linares et al., 2008) were represented as particles with a negative buoyancy. For *P. clavata*, particle density was set to vary between 1.0282 and 1.0295 (a value within this range is randomly sorted at each time step), with an equivalent diameter of 761 μm, to achieve the sinking speed of 0.056 $\pm$ 0.021 cm s^{-1} at 20°C and a salinity of 38 psu as measured experimentally (Guizien et al., 2020). Hence, *P. clavata* larvae behaviour would change according to the surrounding sea water density. For example in summer, they would sink in the upper and lighter part of the ocean but float when dispersed in the deeper and denser ocean layers.

Three levels of vertical subgrid turbulence intensity were tested by repeating each simulation without turbulence, and with a constant low (Munk, 1966, i.e. 10^{-4} m^2 s^{-1}) or

Experiment	Flow horizontal resolution	Flow update frequency	Larval vertical behaviour	Turbulence
Exp.1	Coarse	6 hours	*E. singularis*	No
Exp.2	Fine	6 hours	*E. singularis*	No
Exp.3	**Fine**	**3 hours**	*E. singularis*	**No**
Exp.4	Fine	3 hours	*E. singularis*	Low (10^{-4} m^2s^{-1})
Exp.5	Fine	3 hours	*E. singularis*	High (10^{-3} m^2s^{-1})
Exp.6	Fine	3 hours	*P. clavata*	No
Exp.7	Fine	3 hours	*P. clavata*	Low (10^{-4} m^2s^{-1})
Exp.8	Fine	3 hours	*P. clavata*	High (10^{-3} m^2s^{-1})

Table 1: Larval dispersal simulations setup. Particles were released every hour from June 15 at midnight until July 15 at 11pm for both 2004 and 2006 and tracked for 28 days after release. The total number of particles released each year is 36000 (1 release per hour) for Exp.1, 2 and 3 and 900000 (25 release per hour) for Exp.4, 5, 6, 7 and 8. The reference simulation is indicated in bold.

high (10^{-3} m^2 s^{-1}) turbulent diffusivity (Tab. 1). Depending on whether larval behaviour and/or turbulence was (was not) accounted for, twenty-five (one) particles were released every hour during the entire reproductive period to reach a sufficient number of released particles ensuring the convergence of connectivity matrices (Guizien et al., 2006; Simons et al., 2013).

2.4 Connectivity predictions

Larval transport values between the five locations in the Ligurian sea were calculated as the proportion of particles released during a release event from an origin location that reached a destination location after a given PLD. Release events were defined by their timing and duration. The duration of a release event was varied between 3, 9 and 30 days, the latter representing the entire reproductive period. For each release event duration, a set of non-overlapping release events were built spanning the 30-day long reproductive season of each year (2004 and 2006), yielding twenty 3-day, six 10-day and two 30-day release events. In total, for each of the eight larval dispersal simulation experiments (Tab.1), 252 connectivity predictions were built, varying the PLD (9 levels: 1, 3.5, 7, 10.5, 14, 17.5, 21, 24.5 and 28 days) and the release event duration and timing (3 levels: 3, 9 and 30 days, with 20, 6 and 2 replicates, respectively).

The following metrics were defined to quantify the effect of the release timing variability for each PLD:

$$\sigma_{intra} = \sqrt{\frac{\sum_{y=1}^{Ny}\sum_{r=1}^{N_r}(T_r^y - \overline{T^y})^2}{N_r N_y}} \quad (1)$$

$$\sigma_{inter} = \sqrt{\frac{\sum_{r=1}^{Nr}\sum_{y=1}^{N_y}(T_r^y - \overline{T_r})^2}{N_r N_y}} \quad (2)$$

where N_y is the number of years, N_r is the number of release events per year and $\overline{T^y} = \sum_{r=1}^{N_r} T_r^y/N_r$ is the average connectivity across all release events of year y and $\overline{T_r} = \sum_{y=1}^{N_y} T_r^y/N_y$ is the average connectivity across all years for the release event r in the year. Those metrics decomposed the release timing variability into a within-year (σ_{intra}, standard deviation around the annual mean) and a between-year (σ_{inter}, standard deviation around the release timing mean among years) contribution. Note that in equations (1) and (2), T stands for any element T_{ij} of the connectivity matrix between a release i and destination j location, and a given PLD value. Those metrics were estimated for each pairwise connection among the five locations network. Boxplots were used to display the statistical distribution of σ_{inter} and σ_{intra} in the connectivity matrices for each PLD and release duration in Exp. 1 and 3.

To compare the effects of the flow simulation horizontal resolution and update frequency, of the larval vertical behaviour and of the turbulence level on connectivity predictions within the five-location network, deviations between any experiment and the reference experiment Exp.3 were calculated for each larval transport connection, for a same PLD and release event. The deviations in the different release events were described by their median to avoid any normality assumption. All calculations and statistics were conducted in Matlab (R2018).

3 Results

Exp.1, 2 and 3 were designed to test the usual practice of increasing both spatial resolution and update frequency when considering finer resolution models. In both fine and coarse flow resolution (Exp.1 vs Exp.3), the median connectivity matrix among the five populations displayed a northwestern drift (upper diagonal elements larger than lower diagonal ones), with larval export (off-diagonal elements) from PRV and SES dominating over local retention (diagonal elements) and retention rates dominated over any other connections in BER, POR and PTM for a PLD of 3.5 days (Fig. 2). For the same PLD, varying the update frequency of the fine resolution flow field representation from three to six hours, i.e. same of the coarse resolution simulations (Exp.2 vs Exp.3), did not alter the median connectivity matrix (Fig. S1 in the Supp. Inf.). The sensitivity to update frequency in the fine resolution experiments was negligible across all PLDs (data not shown).

Extending the comparison of Exp.1 and Exp.3 to all PLDs showed that the sets of simulations with different spatial resolution differed largely (Supp. Inf. Fig. S2). Firstly, for short PLDs, larval retention values were ten times larger using the coarse resolution flow representation (max $\sim 95\%$) compared to the fine resolution one (max $\sim 7\%$) with largest retention values found in different locations (BER and POR in the coarse resolution and PTM in the fine resolution; Fig. 2 a,b). Secondly, more connections between populations appeared when the PLD increased using the finer resolution of the flow representation. Finally, connectivity predictions varied little when PLD was varied from 1 to 28 days using the coarser resolution. In contrast, larval transport values decreased drastically when PLD decreased from 1 to 10.5 days and became negligible across the network of the five populations for PLD larger than 14 days using the finer resolution.

Differences in the intensity of coastal currents when varying the resolution of the flow representation explain the differences in larval transport estimates. Coastal currents were weaker in the coarse resolution flow representation compared to the fine resolution one (Figs. S3 and S4 in the Supp. Inf.). For the period May-June 2004, despite the temporal mismatch of the high speed events occurrence, statistically, observed flow speed quantiles

	10%	25%	50%	60%	70%	80%	90%
Observations	3.2	5.9	10.8	13.5	16.6	20.6	26.0
Fine resolution (Exp.3)	4.1	6.8	12.0	14.0	16.2	19.0	24.0
Coarse resolution (Exp.1)	3.2	6.1	9.3	10.5	12.0	14.0	17.6

Table 2: Quantiles of flow speed in cm s^{-1} at the location of the ADCP over a two-month summer period (15/05/2004-15/07/2004) for the observations, and the fine and coarse resolution simulations.

271 corresponding to these events were better predicted in the fine resolution simulation than
272 in the coarse one (Tab. 2).

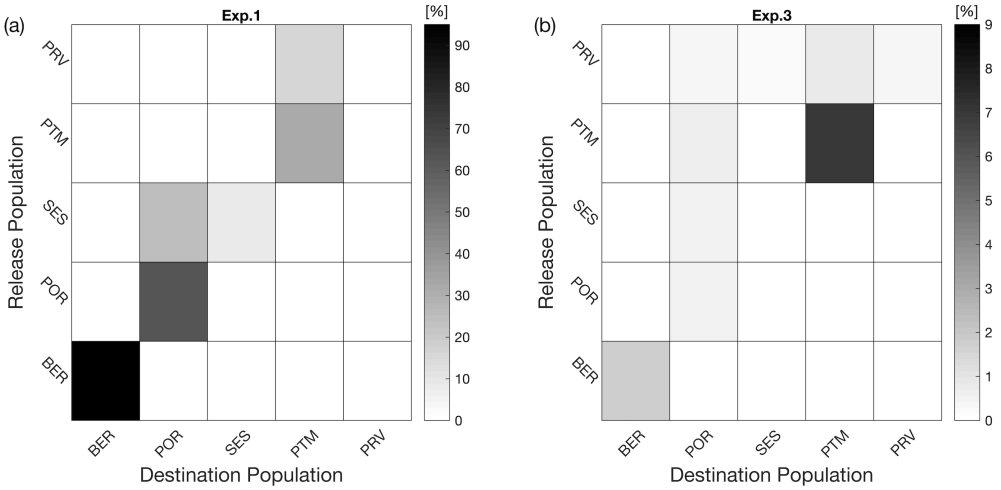

Figure 2: Median connectivity matrix for a PLD of 3.5 days and a 3-day release duration in (a) Exp.1 with coarse resolution flow representation updated every 6h and in (b) Exp.3 with fine resolution flow representation updated every 3h.

273 We then explored the effect on connectivity predictions of the interaction between
274 the flow dynamics simulated at coarse and fine resolution and the larval release timing.
275 Connectivity matrices showed temporal variability at both resolutions. This temporal
276 variability was described by two contributions, the between-year and within-year standard
277 deviation (σ_{intra} and σ_{inter}, Fig. 3 and Fig. S5 of the Supp. Inf.). When larval release
278 timing extended over the entire 30-day reproductive period, the temporal variability
279 equals the between-year variability and was minimum, whatever the flow resolution (Fig.
280 3a and b). Temporal variability increased both between-year and within-year when the
281 release duration decreased, for all PLDs and whatever the flow resolution. Moreover,
282 within-year variability (σ_{intra}) and between-year variability (σ_{inter}) were the same order
283 of magnitude. The within-year to between-year standard deviation ratio was around 1.2

for both resolutions, whatever the release duration and across all PLDs. This indicates that the temporal variability of connectivity predictions can be assessed varying the release timing within a single simulation year. The importance of temporal variability was different in the coarse and fine resolution simulations. In the coarse resolution simulations, the larval transport standard deviation varied little with PLD and reached at maximum 26%, which is a third of the median larval transport. In the fine resolution simulations, the larval transport standard deviation decreased with PLD, and reached up to 100% of the median transfer rates (Fig. S5b vs Fig. 2)).

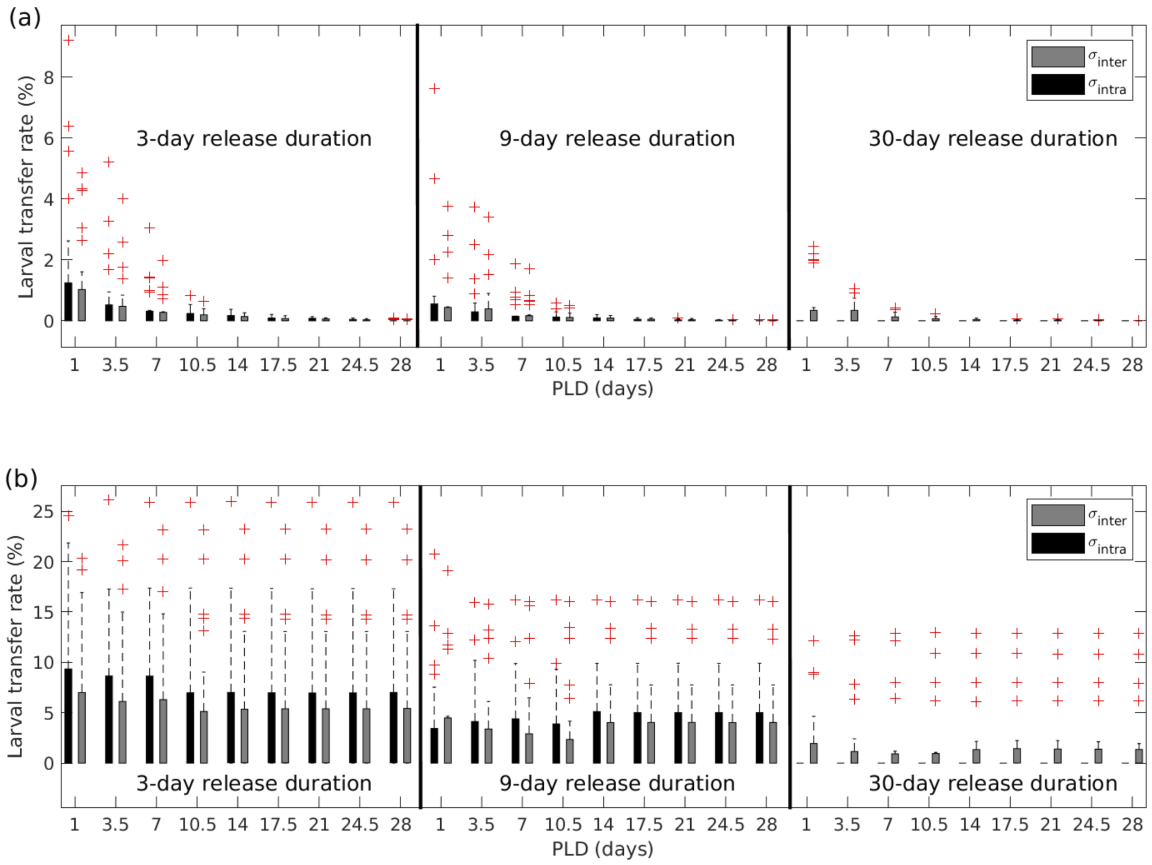

Figure 3: Boxplots of the σ_{intra} (black bars) and σ_{inter} (grey bars) distributions for different PLDs and for different release duration for the Exp.3 (a) and Exp.1 (b) simulations.

The sensitivity of connectivity predictions to other parameters was explored next using the fine resolution flow and quantitatively compared to the sensitivity to horizontal resolution (Fig. 4a and Fig. 5a). Those parameters were the species specific larval vertical behaviour of *E. singularis* and *P. clavata* (Fig.4b and 5b) and different vertical turbulence levels (Fig.4 c,d and 5c,d). A clear hierarchy can be drawn with the effect of the flow

representation resolution being an order of magnitude higher (median deviation up to 90%) than that of incorporating the specific behaviour (median deviation up to 14%) and two orders of magnitude higher than the effect of including turbulence dispersal, whatever the level (median deviation up to 5% for the two levels of turbulence tested, Fig.4c,d). More specifically, the effect of incorporating the specific behaviour of *E. singularis* and *P. clavata* mainly affected the retention rates in PTM, PRV and to a lower extent in SES (Fig.4 b). The effect on all other connections was similarly negligible. The effect of turbulence dispersal only affected retention in PTM (Fig.4 c,d).

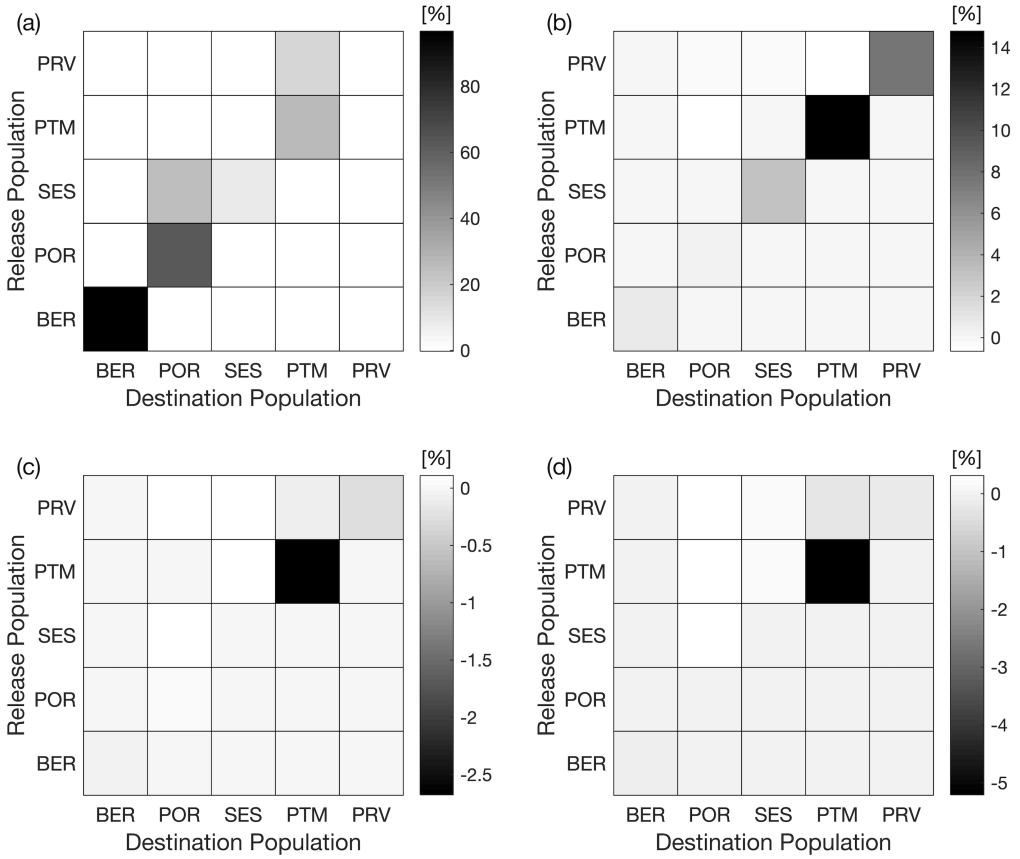

Figure 4: Median of deviation between connectivity matrices in different experiments to the same reference Exp.3 for a PLD of 3.5 days. The different panels display the sensitivity to the resolution of the flow representation (Exp.1 - Exp.3, a), to larval vertical behaviour (Exp.6 - Exp.3, b), to a low vertical turbulence (Exp.4 - Exp.3, c) and a high vertical turbulence (Exp.5 - Exp.3, d).

In particular, larval vertical behaviour affected similarly the spatial structure of connectivity for all simulations with short PLDs and turbulence was always negligible (1-7

days, data not shown). For longer PLDs (10.5-28 days), sensitivity to the specific buoyancy of *E. singularis* and *P. clavata* and to turbulence intensity were significantly reduced, although specific behaviour effect remained prevalent (Fig.5 for a PLD of 28 days). While the specific behaviour continued to affect mainly retention rates when the PLD increase from 3.5 to 28 days (although in different locations, Fig.4b and Fig.5b), the effect of turbulence mainly affected distant connections (import for BER, Fig.5c and d).

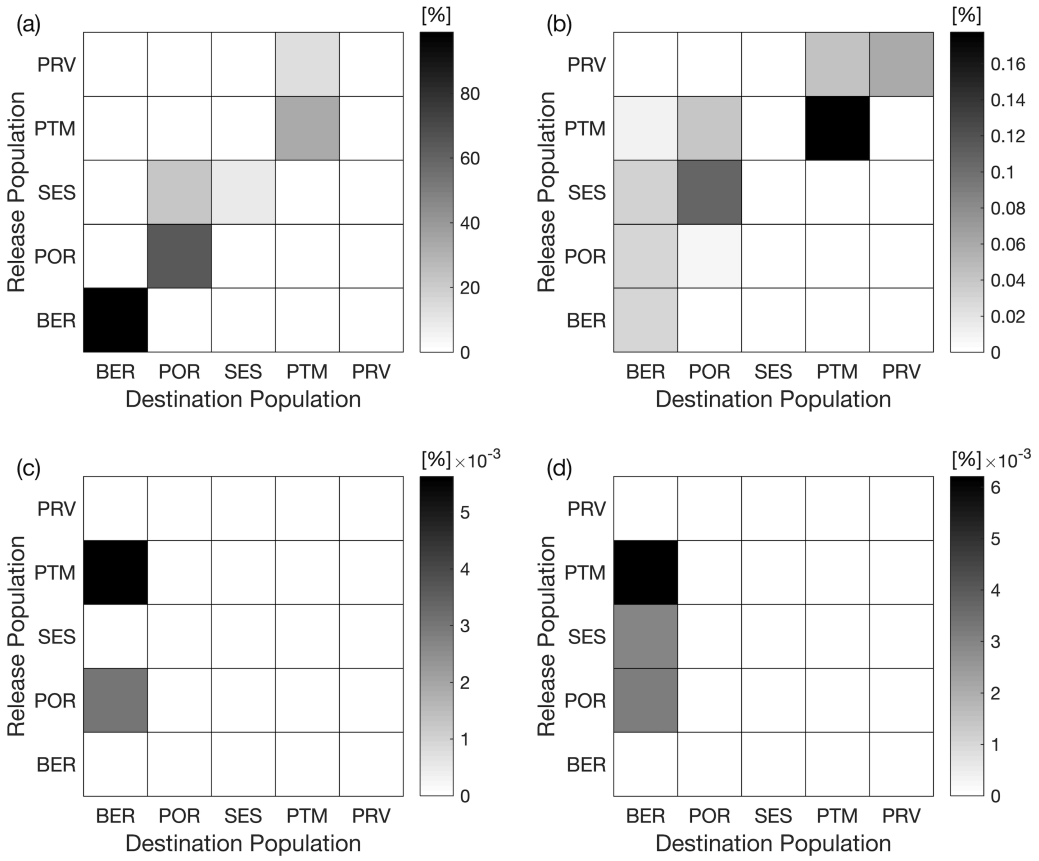

Figure 5: Same as 4 but for a PLD of 28 days

Finally, the sensitivity to larval behaviour and turbulence was compared to the sensitivity to PLD. We selected lower range PLD values (1-7 days) as those are the ones affecting connectivity patterns the most (Fig.S2 in the Supp. Inf.). Varying the PLD from 3.5 to 1 or 7 days affected larval transport estimates of the same order of magnitude as those obtained by incorporating *P. clavata* larval vertical behaviour for the PLD of 3.5 days (Fig.6). Reducing the PLD from 3.5 days to 1 day only increased the retention rates (Fig. 6a) while extending the PLD from 3.5 to 7 days not only decreased retention

rates but also distant connections from SES to POR and from PRV to PTM (Fig. 6b).

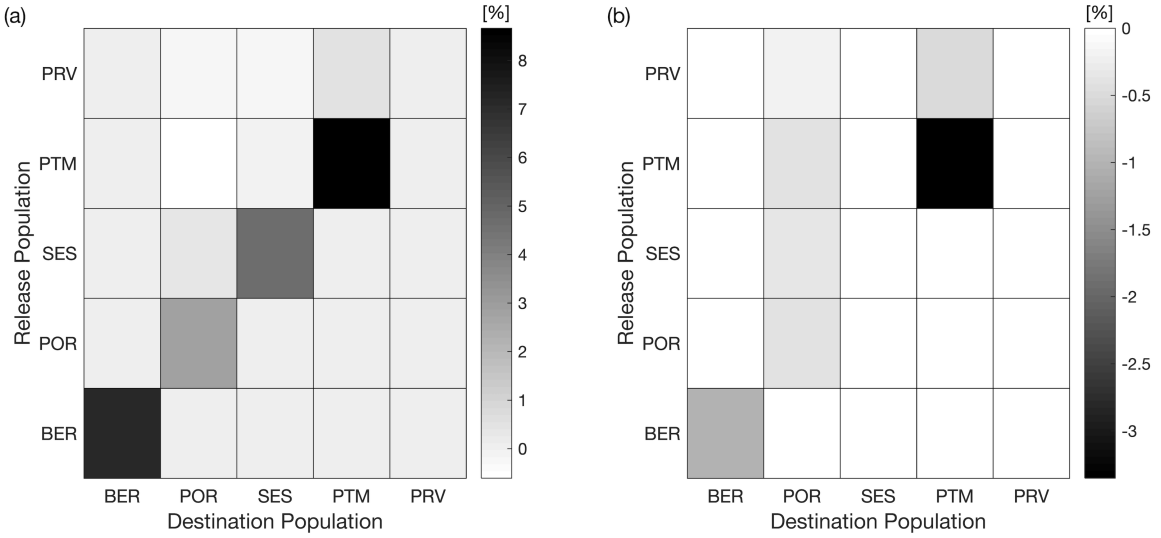

Figure 6: Median of deviation between connectivity matrices in the same reference Exp.3 between (a) a PLD of 1 day, (b) a PLD of 7 days and a PLD of 3.5 days.

4 Discussion

In the present study we tested the sensitivity of connectivity predictions among gorgonian populations dwelling in the Ligurian Sea MPAs to parameters used in larval transport simulations. The horizontal spatial resolution of the hydrodynamical models was found to have the strongest effect on larval transport. Using the finest resolution flow representation, larval behaviour of different gorgonian species and PLD had similar effects on connectivity predictions, while vertical turbulent diffusion was found to have a second order effect. Thanks to the progresses in ocean modelling availability and performances, larval transport predictions are now frequently used to explore the functioning of marine populations and help understanding their spatial distribution (reviewed in Swearer et al. 2019). Assessing the accuracy of larval transport predictions is more than often qualitative (Barbut et al., 2019; Crosbie et al., 2019). However, quantifying the sensitivity of larval transport simulations to the improvements in flow modelling (i.e. flow representation) and larval traits knowledge (i.e. PLD, larval behaviour, release events) is preliminary to assess the accuracy of larval transport predictions and connectivity

patterns used to identify MPAs networks.

The importance of hydrodynamical ocean model spatial resolution in affecting the dispersal patterns of larval transport simulations has been raised in several studies (Guizien et al., 2006; Huret et al., 2007; Putman and He, 2013) and reviewed in Swearer et al. (2019). After comparing two ocean model resolutions of 4 km and 1.6 km, with and without larval vertical behaviour in different years, a recent sensitivity study reported that inter-annual variability was the most influential factor in dispersal simulations of fish larvae in the North Sea (Kvile et al., 2018). The present study showed in contrast that the most influential factor for gorgonian coastal populations in the Ligurian Sea was the flow model resolution as retention increased dramatically when increasing the horizontal cell size from 300 m km to 1.5 km, over-passing the variability of the circulation in two highly contrasting years.

Such bias is to be expected in large scale ocean models when the habitat lies within the coastal boundary layer where the model representation of the flow is inaccurate due to both their coarse resolution and their lack of coastal ocean process parameterization (Griffies and Treguier, 2013). For instance, the internal Rossby radius and the geomorphological features in the North Western Mediterranean coastal zone have dimensions of the same order of magnitude as the coarse resolution used in the present study (Beuvier et al., 2012). The large deviation in connectivity fluxes found in the present study when increasing ocean model resolution advocates to take with caution past studies using basin or Ocean General Circulation ocean Models (OGCM) to evaluate coastal MPAs connectivity (Corell et al., 2012; Andrello et al., 2013). In the present study, despite the coarser resolution of 1.5 km was already four times finer than the one used in these past studies (6-7 km), connectivity among the four Ligurian MPAs varied notably when the resolution was further increased. Specifically, the relative status of the four MPAs changed with Bergeggi and Portofino being the most retentive in the coarse resolution predictions while Punta Mesco became the most retentive in the fine resolution predictions. Another difference was the separation of the four MPAs into three clusters in the coarse resolution predictions while the fine resolution predictions indicate that the three MPAs of

Portofino, Punta Mesco and Porto Venere are connected, Bergeggi being the only isolated MPA. The present study exemplifies the importance of basic methodological choices such as the driving flow representation when science is used to inform management.

Large-scale models have an interest to delineate well-connected oceanic regions, when care is taken of releasing particles outside this artefactual coastal numerical boundary layer (Rossi et al., 2014). Delineating such well-connected regions is essential to identify areas in which ocean circulation downscaled simulations should be performed to study specific populations connectivity. To this respect, including turbulence into dispersal simulations is expected to be less important when the cell size decrease as mesoscale and sub-mesoscale processes will be resolved (Guizien et al., 2006; Huret et al., 2007). In the present study, the effect of vertical turbulent diffusion on connectivity patterns was indeed negligible when resolving the coastal circulation at 300 m compared to the effect of biological traits.

Among biological traits used in larval dispersal simulations, PLD is a basic one as it defines the tracking duration. Several recent works still performed 2D or 3D dispersal varying PLD only (Gamoyo et al., 2019; Hidalgo et al., 2019). In the present study, connectivity predictions varied largely when the PLD varied from 1 to 7 days, but sensitivity to PLD decreased when PLD increased beyond 10 days. Larvae of the few tropical and temperate gorgonian species, whose larval traits have been studied, reached competency after a few days but could survive few weeks in laboratory experiments (Fine et al., 2005; Coelho and Lasker, 2016; Guizien et al., 2020; Zelli et al., 2020). As a result, PLD is a very uncertain parameter in coral species as extended competency seems common for their lecitotrophic larvae thanks to metabolic rate reduction (Graham et al., 2013). In the few larval dispersal modelling studies that targeted gorgonian species, PLDs were varied from a few days to several weeks (Padrón et al., 2018a; Kenchington et al., 2019; Liu et al., 2021). However, despite PLD could extend up to two months, environmental mortality processes occurring during dispersal, such as predation which is removed in the laboratory (Rumrill, 1990), most likely reduce actual PLD in the field. For instance, for the white gorgonian *E. singularis*, the most likely effective PLD determined by comparing dispersal

patterns simulations with population genetics in the Gulf of Lion (Padrón et al., 2018a) lied in the lower range of potential PLDs determined experimentally (Guizien et al., 2020). Similarly, for the red gorgonian *P. clavata*, population genetics indicated short distance dispersal to be the most frequent. Yet, observation of long distance migrants suggests that the larger potential PLD observed in laboratory experiments may also contribute to population genetics (Mokhtar-Jamaï et al., 2011; Guizien et al., 2020). In summary, larval dispersal studies for gorgonian species should systematically assess the sensitivity to PLD over a wide competency window.

It has been recurrently argued that including larval motility behaviour was key to improve the realism of larval dispersal predictions, and led to develop tracking softwares specific for larval dispersal studies (Lett et al., 2008; North et al., 2009; Schlag and North, 2012; Paris et al., 2013). This is considered particularly relevant for the dispersal of fish larvae that can orient themselves and whose swimming speeds are the same order of magnitude as the horizontal flow speed (Leis, 2007, 2021). In contrast, most benthic invertebrates produce larvae unable to outcompete horizontal flow speeds which means passive dispersal in the horizontal (Chia et al., 1984). Yet, larval buoyancy combined to vertical swimming behaviour regulate benthic invertebrate larvae position in the water column, which was shown to alter their dispersal (Guizien et al., 2006; Marta-Almeida et al., 2006; Corell et al., 2012). However, including behaviour in larval dispersal studies of benthic invertebrates remains limited to species with largest vertical swimming speeds such as the diel vertical migration of crustacean species (Queiroga et al., 2007), and oysters (North et al., 2008) or scallops (Tremblay et al., 1994). When larval vertical behaviour was assumed negligible, two dispersal procedures, either two-dimensional at fixed depth or three-dimensional driven by flow vertical velocities have been used. These have been indifferently termed "passive" (Gamoyo et al., 2019; Kenchington et al., 2019; Metaxas et al., 2019). Actually, none of these dispersal simulation approaches should be termed "passive", as both implicitly assume a larval vertical behaviour with continuous adjustment of larval buoyancy to varying surrounding sea water density. The present study exemplifies that moderate differences in larval vertical behaviour in two gorgonian

species, one passive drifter represented by negative buoyancy and the other active swimmer represented by neutral buoyancy, varied retention in the populations of Porto Venere, Punta Mesco and Sestri Levante. This result suggests to re-cast previous estimates based on two-dimensional dispersal at a prescribed depth for those same species (Rossi et al., 2020). Recent knowledge advances about larval vertical behaviour within the subset of gorgonian species should encourage us to re-cast connectivity predictions including behaviours explicitely in dispersal simulations (Coelho and Lasker, 2016; Guizien et al., 2020).

Release duration is another reproductive trait that was shown to affect the stability of connectivity patterns (Guizien et al., 2012; Hock et al., 2019). Release duration varies largely among gorgonian species from synchronized short pulses in spawning species (Coma et al., 1995; Coelho and Lasker, 2016) to continuous release in brooding species (Coelho and Lasker, 2014). In the two gorgonian species considered in the present study larval release happens in a few short pulses which timing varies between years during the reproductive season and seems unpredictable (Coma et al., 1995; Ribes et al., 2007). The present study showed that such traits result in uncertain connectivity predictions, which variability can be equally estimated using within- or between-year statistics. A similar increase in connectivity predictions variability when release duration decreased was already reported in the Gulf of Lion, a region displaying similar short-term atmospherical variability to the Ligurian Sea (Vignudelli et al., 1999; Briton et al., 2018). Moreover, for the two gorgonian species in the Ligurian Sea considered in this study, sensitivity to release timing could reach up to 100% of median larval transport values and was the same order of magnitude as to sinking behaviour. As a consequence, connectivity predictions in these two gorgonian species will remain unstable, despite larval behaviour is better ascertained, making cross-validation with observed population genetics more hazardous (Padrón et al., 2018b,a).

In conclusion, methodological choices are crucial when performing larval dispersal simulations to guide biodiversity management. Specifically, advising the design of coastal MPA with adequate regional connectivity estimates requires adapting flow simulation

resolution to the area. For species dwelling in rocky habitat such as gorgonians, flow representation at a grid resolution sufficient to resolve the coastal dynamics in these environments is a bottleneck, and despite coastal dynamics may be very different from place to place, the bathymetry steepness is likely to require horizontal resolution in the order of a few hundred meters or less. In such a case, multiplying dispersal tracks to account for turbulence effect can be avoided as the flow representation will already include most of the subgrid variability, reducing computational costs. In contrast, estimating dispersal patterns variability arising from uncertainty on release timing by simulating multiple release events and PLD range should be systematic to estimate confidence level for the different connectivity patterns. These initial methodological choices do not preclude the need to vary the larval vertical behaviour when known to span the range of variability arising from species diversity.

Supporting Information

Supporting Information are available in online version of the manuscript.

Acknowledgments

This work was supported by the IMPACT EU funded project (PC Interreg VA IFM 2014-2020, Prot. ISMAR n. 0002269). The authors would also like to thank Francesco Ferrari, Federico Cassola and Andrea Mazzino for providing the surface forcings for the LIMEgcm setup used in this work and Anna Vetrano and Mireno Borghini for the ADCP data collected in proximity of the MT Haven shipwreck. The data underlying this article will be shared on reasonable request to the corresponding author.

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Supporting Information

Location (name code)	Longitude [deg. E]	Latitude [deg. N]	Coarse Resolution Depth [m]	Fine Resolution Depth [m]
Bergeggi (BER)	8.4550	44.2399	-28	-88
	8.4550	44.2349	-32	-102
	8.4550	44.2449	-24	-52
	8.4550	44.2299	-36	-133
	8.4550	44.2499	-22	-25
	8.4450	44.2249	-25	-133
	8.4600	44.2399	-36	-110
	8.4500	44.2249	-32	-150
	8.4600	44.2449	-31	-90
	8.4600	44.2499	-29	-75
Portofino (POR)	9.2200	44.2899	-27	-52
	9.2150	44.2899	-24	-38
	9.2250	44.2899	-34	-63
	9.2100	44.2899	-22	-26
	9.2349	44.299	-31	-63
	9.2200	44.2849	-36	-75
	9.2349	44.3049	-24	-52
	9.2349	44.2949	-38	-63
	9.2150	44.2849	-32	-63
	9.2100	44.2849	-30	-50
Sestri Levante (SES)	9.3950	44.2449	-34	-9
	9.3900	44.2499	-33	-12
	9.4000	44.2449	-29	-12
	9.3900	44.2549	-26	-3
	9.4000	44.2399	-38.	-33
	9.4050	44.2449	-23	-3
	9.3850	44.2549	-32	-12
	9.3850	44.2599	-24	-7
	9.4050	44.2399	-31	-26
	9.3800	44.2549	-38	-25
Punta Mesco (PTM)	9.6300	44.1199	-20	-33
	9.2500	44.1199	-22	-30
	9.6300	44.1149	-28	-42
	9.6200	44.1199	-28	-33
	9.6250	44.1149	-30	-52
	9.6350	44.1149	-26	-42
	9.6200	44.1149	-38	-52
	9.6400	44.1149	-24	-25
	9.6300	44.1099	-35	-52
	9.6150	44.1199	-35	-42
Porto Venere (PRV)	9.8350	44.0149	-21	-12
	9.8400	44.0099	-21	-18
	9.8500	44.0049	-22	-18
	9.8550	44.0049	-21	-18
	9.8450	44.0049	22	-18
	9.8350	44.0099	-24	-18
	9.8599	44.0049	-20	-18
	9.8400	44.0049	-24	-18
	9.8300	44.0149	-23	-12
	9.8350	44.0049	-26	-18

Table S1: Longitudes, latitudes and depths of the release points for each population in the Ligurian Sea. Longitudes and latitudes are the same for both models while depths vary between the fine and coarse resolution model.

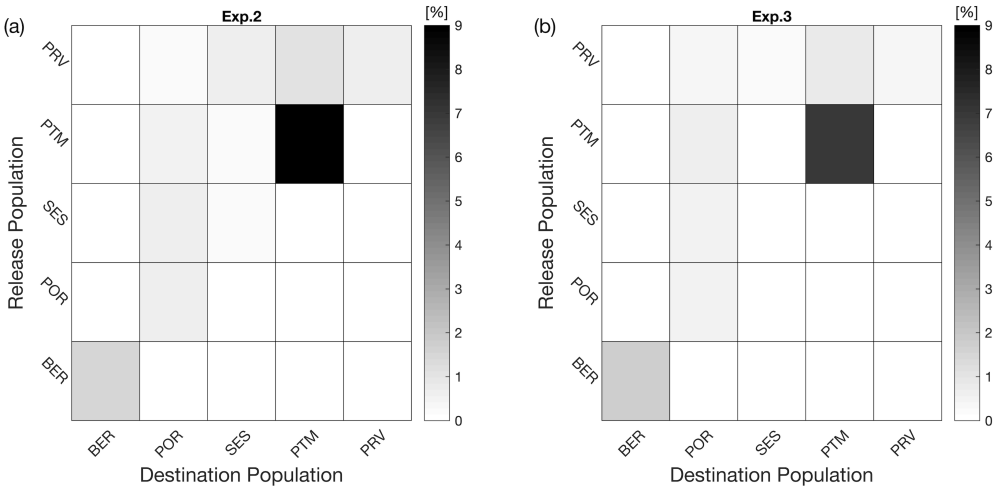

Figure S1: Median connectivity matrix for a PLD of 3.5 days and a 3-day release duration in (a) Exp.2 with fine resolution flow representation updated every 6h and in (b) Exp.3 with fine resolution flow representation updated every 3h.

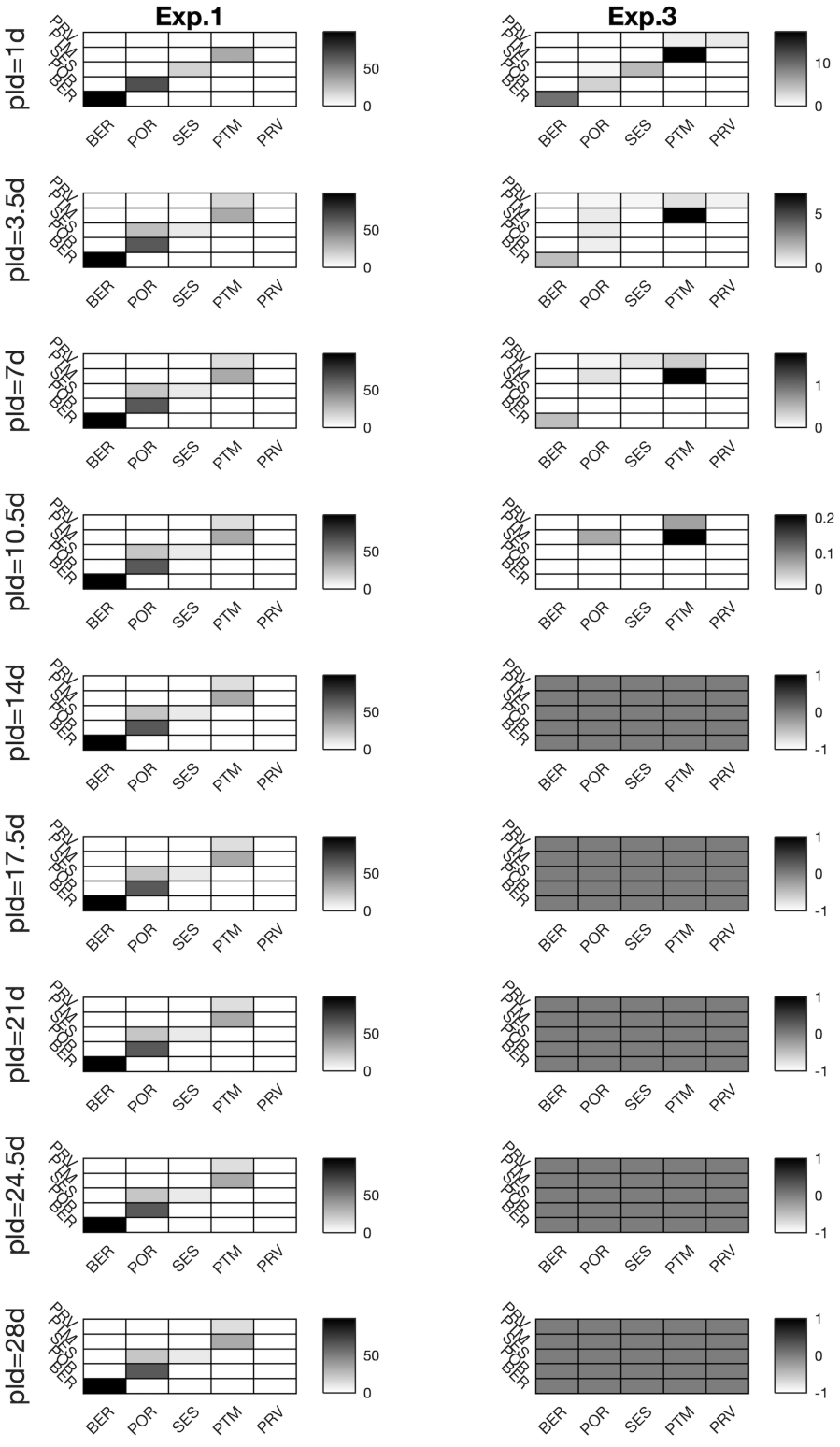

Figure S2: Median connectivity matrix for all PLDs and a 3-day release duration. The panels on the left display Exp.1 with coarse resolution flow representation updated every 6h and the panels on the right display Exp.3 with the fine resolution flow representation updated every 3h.

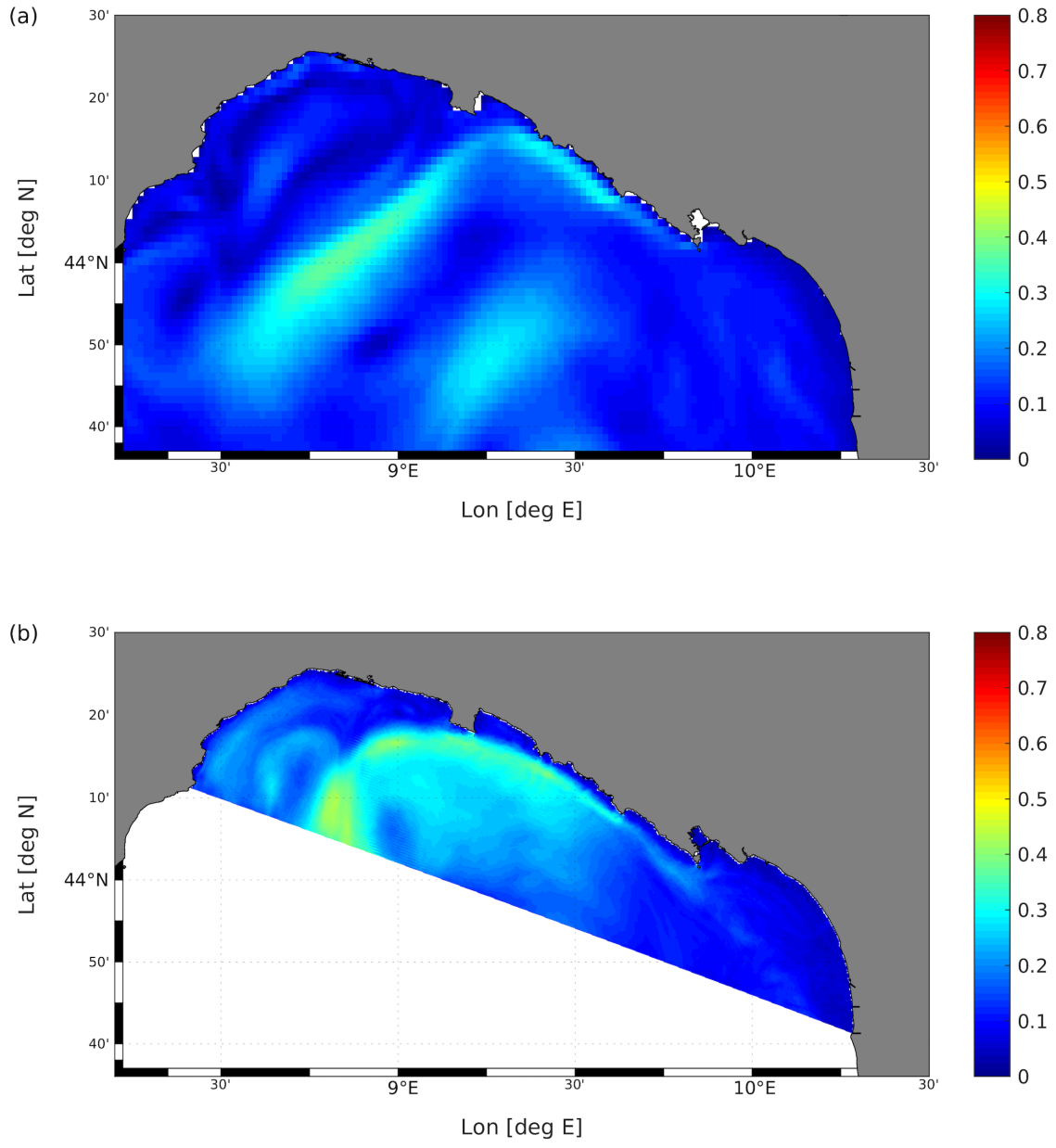

Figure S3: Surface speed on June 30th 2004 simulated at (a) coarse and (b) fine resolution.

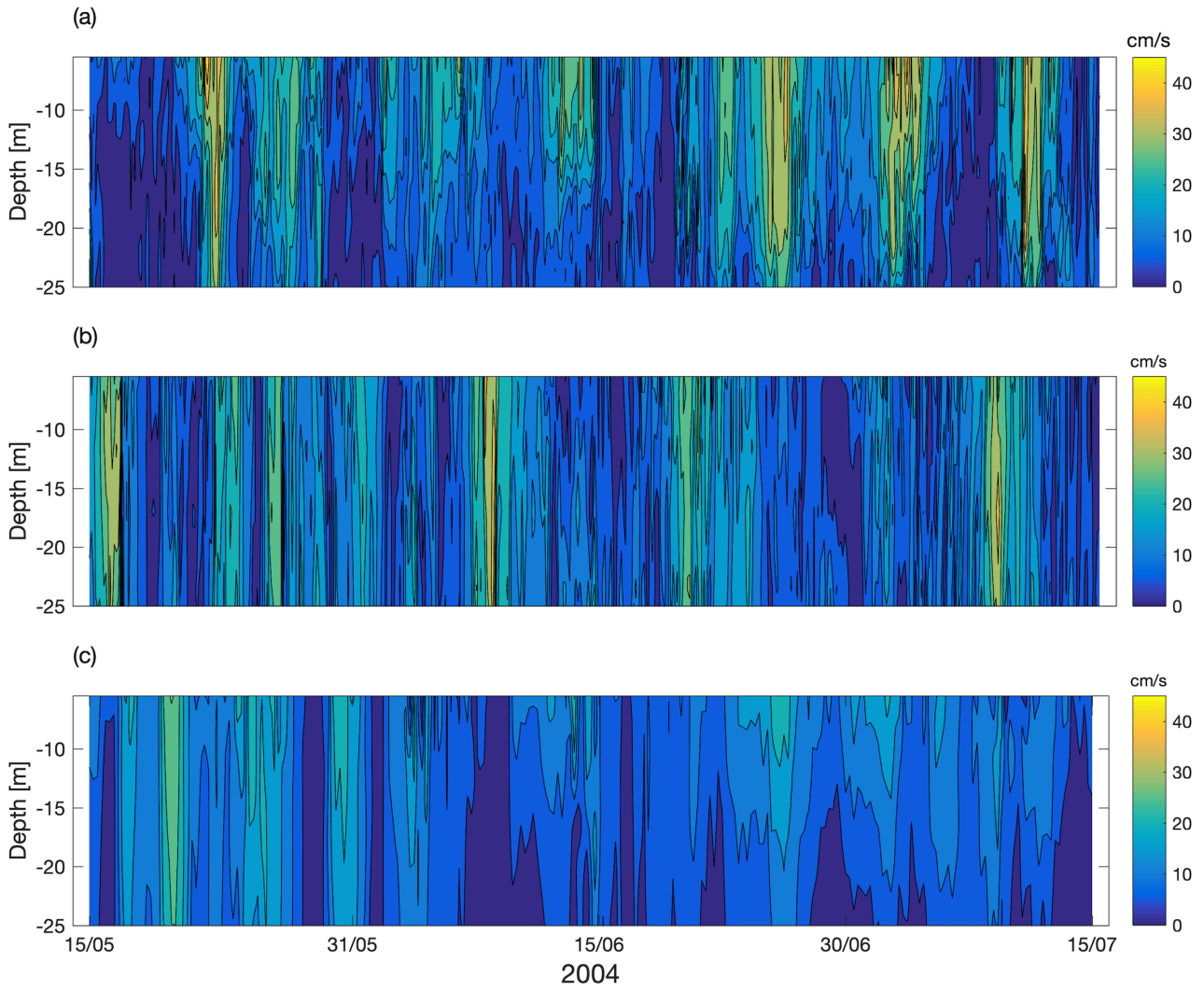

Figure S4: Current as a function of depth and time (15/05/2004-15/07/2004) in (a) observations, (b) the fine resolution 3D flow simulation, (c) the coarse resolution 3D flow simulation. Observations were taken from an Acoustic Doppler Current Profiler (ADCP) located in the vicinity of the MT Haven shipwreck in the Ligurian Sea (44.37N, 8.70E). Flow simulation data are obtained from the closest grid points to the ADCP location.

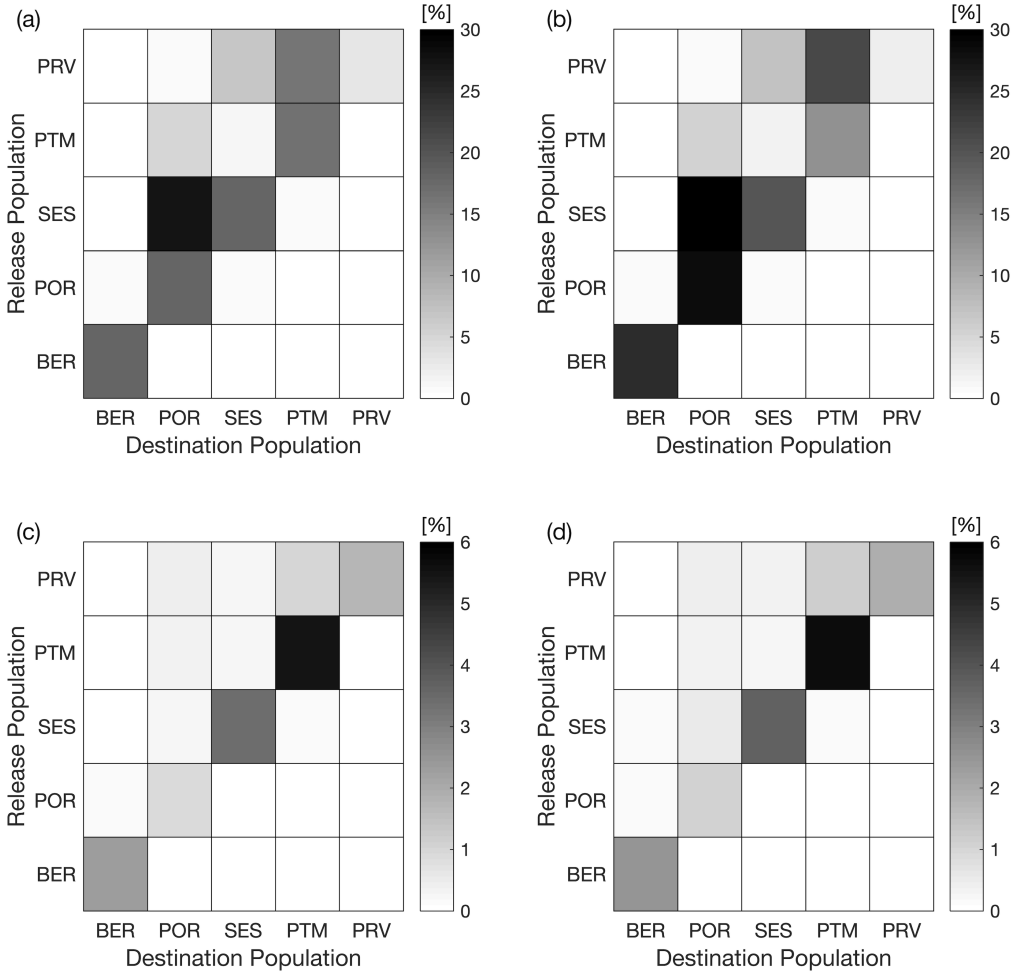

Figure S5: Connectivity matrix for the larval release events of 2004 and 2006 for the *E. singularis* behaviour simulations without turbulence and a PLD of 3.5 days. Panels (a) and (b) represent the σ_{intra} and σ_{inter} for Exp.1, panels (c) and (d) represent the σ_{intra} and σ_{inter} for Exp.3.